

CHARACTERISTICS AND LIFE-HISTORIES OF YORKSHIRE ACULEATES

Michael Archer

The aculeate wasps, ants and bees belong to the insect order Hymenoptera, with about 6,500 species in the UK. Hymenoptera are characterised by usually having two pairs of membranous wings, of which the fore pair are larger. The front margin of the hind wings has a row of hooks by which the hind wings can be hooked to a fold on the hind margin of the fore wings. In this way the two wings on each side of the thorax act as a single membrane in flight. In addition the first segment of the abdomen has become closely associated with the thorax and is called the propodeum. The rest of the abdomen, minus its first segment, is called the gaster.

The U.K. Hymenoptera fauna consist of three groups: the sawflies and wood wasps (about 470 species), parasitic wasps (about 5,500 species) and aculeates (about 570 species). The parasitic wasps and aculeates can be distinguished from the sawflies and wood wasps in having a distinct 'waist' between the propodeum and the gaster. The aculeates can be separated from the parasitic wasps by their ovipositors which are modified to form a sting. Aculeates lay their eggs through a slit at the base of the sting, allowing the sting to be used for defence and for paralysing and sometimes killing their prey. Aculeates have evolved many morphological modifications to their bodies and behaviour patterns to assist in collecting food and providing a protective nest with cells for the brood stages. Gauld & Bolton (1996) give further information and illustrations on the morphology of adults.

Higher classification of the aculeates

For this introduction three superfamilies are recognised: Chrysidoidea, Vespoidea, Apoidea (Gauld & Bolton, 1996). The Chrysidoidea consists of four families: Bethyridae, Chrysididae, Dryinidae and Embolemidae, and the Vespoidea of six families: Formicidae, Mutillidae, Pompilidae, Sapygidae, Tiphiidae and Vespidae). The Vespidae consist of the subfamilies Eumeninae and Vespinae. The Apoidea can be divided into eight families (two families of wasps: Sphecidae and Crabronidae, and six families of bees: Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae and Apidae). Bees of the Apidae have been divided into seven subfamilies: Colletinae, Andreninae, Halictinae, Melittinae, Megachilinae, Anthophorinae and Apinae (Gauld & Bolton, 1996). Bohart & Menke (1976) in a world survey also treated the apoid wasps within the single family, Sphecidae. However, Michener (2000) in a world survey of the bees treated the above subfamilies as families except the Anthophorinae and Apinae which were grouped together as the family Apidae.

The varieties of aculeate life histories

The food provided by females for their larvae is either animal-based, as in the wasps, or plant-based as in the bees. Some species have evolved to use the food stored by another species in a 'cleptoparasitic' way of life. The cleptoparasitic female does not make a nest but places its egg on the prey, pollen store or inside wall of the cell of a host species. The cleptoparasitic female may also destroy the egg of the host species, but more usually the cleptoparasitic larva, just after hatching, destroys the egg or young larva of its host. The

cleptoparasitic larva then eats the provisions provided by the host female. Some species have a parasitoid life history: the parasitoid female places its egg so that on hatching it can feed upon the mature larva or pupa of its host.

Most species of aculeates have a solitary life-history in that each female makes her own nest (if a nest is made) and provides food for her offspring. After a cell has been mass provisioned, an egg is laid and the female leaves. Some species of solitary wasps and bees make their individual nests close to each other, maybe because of a shortage of appropriate nesting space, so that the nests appear as an aggregation. Nesting in aggregations and the increased adult activity may deter the entry of parasites, cleptoparasites and predators into nests. Aggregations may also arise because females return to nest in the natal nesting area, or even in their natal nests.

Aggregation nesting could evolve into communal nesting where several females of the same generation each build a separate nest but use a common entrance. The females do not co-operate in the rearing of each other's brood, but there could be beneficial consequences; there is a reduction in burrow excavation besides the increased difficulty for parasites and predators to enter the nest complex.

Where females show co-operative behaviour in rearing each other's brood they are called quasisocial species. In semisocial species closer co-operation between the females occurs with a reproductive division of labour. In subsocial species the female does not desert her brood at the egg stage but remains to guard the brood and provide food for her larvae as it is needed - gradual or progressive provisioning. The female then deserts. However if the female continues to remain with her brood until they emerge as adults then there is an overlapping of two generations, and the possibility of co-operation between parent and offspring. With such co-operation and a reproductive division of labour the state of eusociality has been reached.

Eusocial species show the following three characteristics:

1. Individuals of the same species co-operate in caring for the brood.
2. There is a reproductive division of labour with more-or-less sterile workers and fecund queen(s).
3. There is an overlap of at least two generations capable of contributing to colony labour.

If there is little or no morphological difference between the queen(s) and the workers then the species are called 'primitively eusocial'. If there are marked morphological differences between the queen(s) and workers then the species are called 'advanced eusocial'. The difference between solitary and social species is therefore not clear-cut but usually 'social' species is used to refer to eusocial species while species intermediate between solitary and eusocial species are called 'presocial' species.

In the following account, size is based on body length as follows: very small (less than 3mm), small (3-6mm), medium (6-10mm) and large (over 10mm).

Six aculeate divisions

Aculeates can be arbitrarily divided into six groups based on recording procedures and life-history differences: the DEB group, solitary wasps, solitary bees (including a few eusocial species), social wasps, social bees and ants which are all social. In the following accounts the

list of species recorded from 2000-2019 are given followed by the other species that have recorded with the last year in which they were recorded. (E) indicates that a species is extinct or probably extinct in Yorkshire.

Pictures and British and Irish distribution of most species can be found on the web site:
www.bwars.com

The DEB group consists of three families: Dryinidae, Embolemidae and Bethyridae. The Dryinidae, and probably the Embolemidae, show a parasitoid life style. The female stings the host producing temporary paralysis before laying an egg. The larva, on hatching from the egg, partly or entirely enters the body of its host on which it feeds, eventually killing it. The Bethyridae show an ectoparasitoid life style, although they are normally referred to as predators. The female stings the host producing permanent paralysis or even death. The prey is then dragged to a secluded place when one or two eggs are laid on the prey. The female then leaves.

Family **Dryinidae**

Very small solitary wasps. Black, sometimes with lighter colours, e.g. brown, yellow, ivory, white. Males are winged. Females may be winged, wingless or with reduced wings. The adults are active from April until September, but mainly during the summer months. They are parasitoids on nymphal, rarely adult, Auchenorrhyncha Homoptera of the families Cicadellidae and Delphacidae. The female approaches the host which is gripped either by the pincer-like chelae of the fore leg, or for *Aphelopus*, by the fore and middle legs. The host is stung into temporary paralysis. An egg is laid between two of the host's abdominal segments. The host normally recovers and continues to move about. The egg hatches into a larva which feeds on the host. Feeding may be externally on or internally within the host. Later instars may develop outside the host within a sac, projecting from the abdomen of the host. The sac is formed of the cast skins of the developing larva. For *Aphelopus* the sac consists of a proliferation of the host's tissue and cast skins. The sac is often different in colour from the host. The larva eats out the contents of its host resulting in its death. The larva pupates in the soil or on the food plant of the host. The cocoon is made of very dense silk. Over-wintering is usually in the pupal stage. There may be one or two generations a year. Nationally: 7 genera with 34 species. 23 species in 4 genera currently present in Yorkshire. Many of the species were recorded in the 1990s and are still present in the 2000s. The DEBs have recruited very few recorders.

Aphelopus atratus (Dalman), *A. melaleucus* (Dalman), *A. nigriceps* Kieffer,
A. serratus Richards.

Anteon ephippiger (Dalman), *A. flavicorne* (Dalman), *A. fulviventre* (Halliday),
A. gaullei Kieffer, *A. infectum* (Halliday), *A. jurineanum* Latreille, *A. pubicorne* (Dalman),
A. scapulare (Halliday).

Lonchodryinus ruficornis (Dalman).

Aphelopus quercus Olmi, 1992.

Anteon arcuatum Kieffer, 1993; *A. brachycerum* (Dalman), 1991; *A. exiguum* (Haupt), 1986;
A. tripartitum Kieffer; 1995.

Gonatopus bicolor (Halliday), 1992; *G. clavipes* (Thunberg), 1990; *G. distinctus* (Kieffer),
1991; *G. distinguendus* (Kieffer), 1986; *G. lunatus* (Klug) 1985.

Family **Embolemidae**

Small reddish-brown solitary wasps. Males are winged and the females wingless. The adults are active from August until October and the females again during April and May. One British species with an unknown natural history also currently present in Yorkshire. A North American species is a parasitoid on a fulgorid homopteran with a dryinid-like life history.

Embolemus ruddii Westwood. 1990.

Family **Bethylidae**

Very small solitary wasps. Males winged, rarely reduced. Females winged, wingless or with reduced wings. Adults usually black. The adults are active from April until October, but mainly during the summer months. They are external parasitoids on beetle or lepidopterous larvae. The host is rapidly paralysed and may be killed. It may be dragged or carried to a concealed place, or may already be in a concealed place, e.g. within rolled leaves or under bark. One or more eggs are laid on the host. The female may feed on the haemolymph that oozes from the sting punctures. The larvae feed externally on the host. The female may stay with the larvae until they mature. More than one generation may be reared on a large host. Females probably over-winter as adults.

Nationally: 8 genera with 15 native species, with a further species restricted to the Channel Islands, and several introduced species associated with granaries and storehouses. 4 species in 2 genera currently present in Yorkshire.

Bethylus fuscicornis (Jurine).

Cephalonomia formiciformis Westwood. 1991.

Bethylus cephalotes Förster, 1999; *B. dendrophilus* Richards, 1987;

Solitary and Social Wasps and Ants

The solitary wasps consist of the seven families: Chrysididae, Tiphidae, Mutillidae, Sapygidae, Pompilidae, Sphecidae and Crabronidae, and one subfamily, Eumeninae. Each family or group of species specialises in a particular type of prey, e.g. spiders, aphids, caterpillars. Like the Bethylidae, some species of solitary wasps do not build a nest for their brood. Often, however the prey is already in a concealed space. The cleptine (Chrysididae) female chews a hole through the cocoon of its prey, a sawfly pupa, on which she lays an egg. Other chrysidids, sapygids and mutillids lay their eggs in the cells of other aculeate species. The tiphids lay their eggs on beetles in their subterranean burrows. The sapygids are cleptoparasites on megachiline bees.

Some sphecids and pompilids drag their prey to a natural crevice like a beetle boring in wood or a hollow stem before laying an egg. The crevice is then sealed. Other sphecids and pompilids, after capturing their prey, temporarily conceal them before excavating their nests. Yet other sphecids and pompilids build their nests first before capturing prey. Cells are filled with one or several prey (mass provisioning). An egg is laid on the prey and the cell sealed. Eumenines lay their egg in the cell before the cell is mass-provisioned with prey. A few sphecids only provision the cell with a limited amount of prey, adding more prey as the larva grows (progressive provisioning) - the cell may be sealed between successive provisionings.

The nests may be underground or aerial in hollow stems, old beetle borings in wood, nail holes in fence posts, or exposed on plants or hard surfaces. The burrow may lead to a single or several cells. The prey may be permanently paralysed or killed. A few species are cleptoparasitic on other solitary wasp species. Hunting for prey and nest building is carried out by the females.

Family **Chrysididae**

These solitary wasps are often called cuckoo, or ruby-tailed, wasps. They have a heavily-armoured, brightly-coloured cuticle. The apical gastral segments have been modified to form a thin, tubular structure that can be telescoped into the hind end of the gaster. In the female this tubular structure has been secondarily modified to act as an ovipositor. They have a parasitic life-history.

Subfamily **Cleptinae**

Small brightly coloured wasps. The female has four visible gastral segments and the male five visible segments. The female searches for the cocooned prepupa or pupa of a tenthredinid sawfly. On finding a host cocoon the female bites a small hole in the wall. She then inserts her ovipositor and lays a single egg on the prepupa or pupa. The hole is sealed with mucilage and the larva, on hatching, feeds on the host. Nationally: 1 genus with 2 species, 1 species currently present in Yorkshire.

Cleptes semiauratus (Linnaeus).

Cleptes nitidulus Fabricius, 1850. (E)

Subfamily **Chrysidinae**

Small to medium-size wasps. Cuticle brightly metallic-coloured which may be purple, blue, green and red. The female and male have three visible gastral segments. Their hosts belong to aculeate subfamily Eumeninae and family Sphecidae. The hosts nest in the ground, in cavities in wood and in mud cells attached to a firm structure such as a wall. The female enters the host's nest and lays an egg in each available cell. On hatching, the larva usually eats the egg or young larva of the host, before the food store (cleptoparasitic life-history). In some species the larva feeds only on the larva of the host and eventually kills it (parasitoid life-history). Adults can adopt a rolled-up defensive posture when threatened. Nationally: 11 genera with 38 species. 17 species in 7 genera currently present in Yorkshire.

Elampus panzeri (Fabricius)

Hedychridium ardens (Latreille),

Pseudomalus auratus (Linnaeus), *P. violaceus* (Scopoli).

Chrysis angustula Schenck, *C. corusca* Valkeila, *C. ignita* (Linnaeus), *C. impressa* Schenck,

Chrysis ruddii Shuckard, *Chrysis vanlithi* Linsenmaier, *C. viridula* Linnaeus.

Chrysura radians (Harris).

Trichrysis cyanea Lichtenstein.

Omalus aeneus (Fabricius). 1997.

Hedychridium cupreum (Dahlbom), 1997.

Chrysis mediata Linsenmaier, 1948. (E).

Family **Tiphiidae**

Subfamily **Tiphiinae**

Small to large, black, solitary wasps. The larvae of this species are parasitoids on scarabaeid beetle larvae (*Aphodius*, *Rhizotrogus*, *Anisoplia*). The female burrows into the soil to find a usually mature larval host in its cell. The wasp burrows below the host's cell before breaking into it, where she stings the larva and kneads it with her mandibles. An egg is laid usually on the lateral or ventral surface of the host in a fold of the cuticle. The paralysis is temporary, lasting 20-40 minutes, after which the larva becomes active, usually sufficiently so to continue feeding on grass roots. The larva takes about three weeks to eat its host. Pupation takes place in the host's cell. Probably one generation a year. Nationally: 1 genus with 2 species. Currently 2 species present in Yorkshire.

Tiphia femorata Fabricius, *T. minuta* Van der Linden.

Subfamily **Methochinae**

Medium-size black, solitary wasps with the female having a red thorax, propodeum and part of the antenna. Female wingless. The larvae are parasitoids on larvae of tiger beetles (*Cicindela*). The female runs over the surface of the ground looking for the burrow of its host. When found, the wasp allows the host's larva to grasp her around her heavily-armoured thorax. As the host comes out of its burrow the wasp bends its gaster down and stings the larva below the head capsule. The larva is quickly immobilised and the wasp then pulls it deep into the burrow where she lays a single egg on the ventral side, usually behind the coxae of the hind legs. The wasp fills the burrow with grains of sand, small twigs and small fibrous pieces of humus before leaving. Probably one generation a year. Nationally: 1 species, also currently present in Yorkshire.

Methocha articulata Latreille.

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Family **Mutillidae**

Subfamily **Myrmosinae**

Female small and male small to medium-size solitary wasps. The male is black and the female red with a black head and black bands on the gaster. Female wingless. The larva is probably a parasitoid, rather than a cleptoparasite, on various ground-nesting sphecid wasps and halictid bees. The female runs over the surface of the ground searching for the burrows of its hosts. Nationally: 1 species, also currently present in Yorkshire.

Myrmosa atra Latreille.

Subfamily **Mutillinae**

Medium-size to large solitary wasps. Black with much of the thorax red and bands of silvery hairs on the gaster. The larva is a parasitoid on various ground-nesting wasps and bees. Nationally: 2 genera with 2 species. Currently 1 species in Yorkshire.

Mutilla europaea Linnaeus, 1758.

Family **Sapygidae**

Medium-size to large wasps. Black, often with red, yellow or white markings. The larvae are cleptoparasites on solitary bees of the genera *Osmia* and *Chelostoma*. The female introduces

an egg into the cell of its host by using her sting to penetrate the cell wall. On hatching, the first instar larva, although without legs, is active and destroys the host's egg with its large mandibles. The larva then moults into the next instar which has smaller mandibles and feeds on the host's provisions. Probably one generation a year. Nationally: 2 genera with 2 species, both currently present in Yorkshire.

Sapyga quinquepunctata (Fabricius).

Monosapyga clavicornis Linnaeus. 1996

Family **Formicidae**

The advanced eusocial ants have diverse life-cycles lasting more than one year. Their nests are found in dead wood, or, more usually, in the soil, often under a stone, or raised above the ground in a mound of earth or plant debris. Typically, the colony consists of one or more queens with a large number of workers and brood. Males and new queens are reared seasonally. The most common life-cycle starts with the mating flight after which the males die and the fertilised queens shed their wings and enclose themselves in an earthen cavity. Eggs are laid and the larvae are fed by the queen on the degeneration products of her flight muscles. The first brood consists of workers which help the queen to rear further broods. The larvae are fed by the workers on a wide variety of foods of animal and vegetable origin. The larvae are housed in chambers built by the workers. Pupation occurs within the chambers. Adult emergence from the cocoons, when present, usually cannot take place without assistance from the workers. When the colony reaches a certain size new queens and males are reared. The colony, however, does not end with the production of the sexuals but can continue for several years rearing further sexual broods. This basic life-cycle can show variations. The newly mated queen may return to the natal colony rather than starting a new colony. Such colonies eventually undergo fission with queens and workers leaving the parent colony to form a new colony. In some species, the newly mated queen penetrates the colony of a different species, usually killing the host queen. The intruder queen lays her eggs which are reared by the host workers. The workers of the intruder queen gradually replace the host workers which eventually all die. Such a life-cycle is call 'temporary social parasitism'. In 'permanent social parasitism' (or inquilinism) the intruder queen generally does not lay eggs that become workers, but only lays eggs which become new queens or males, like the social parasites of social wasps and bees.

Genus **Myrmica** Latreille, 1804

Yellowish-brown, blackish-brown to reddish-brown ants. Queens medium-size, workers and males small. Nesting in tree stumps, under stones or in banks. Colonies are relatively small with one or a few queens, and from a few hundred to at least 1000 workers. Forage on the ground and 'milk' aphids. Mating flights occur during the summer. Nationally: 12 species with 6 species in Yorkshire.

M. rubra (Linnaeus), *M. ruginodis* Nylander, *M. sabuleti* Meinert, *M. scabrinodis* Nylander, *M. sulcinodis* Nylander.

M. lobicornis Nylander, 1992.

Genus **Leptothorax** (Mayr, 1855)

Reddish to brownish-yellow, to almost black, small ants. Colonies with one to several queens and 25-60 workers. Subterranean nesters in open woodland and moorland, in places such as under dry peat, rock crevices, under stones and bark, and in fallen trees. Mating flights in July. Workers are predatory on small insects and also scavenge on dead insects. Nationally: 5 species, including 1 species restricted to the Channel Islands. 1 species in Yorkshire.

Leptothorax acervorum (Fabricius), 1996.

Genus **Lasius** Fabricius, 1804

Yellow to black ants. Queens medium-size, workers and males small. They forage for honeydew from aphids but are also carnivores and scavengers. Subterranean nesters, but also in tree stumps and old walls, forming large colonies with one to several queens and a few hundred to a few thousand workers. Workers of *L. flavus* seldom come to the surface. *L. niger* founds new colonies by a single queen and *L. flavus* by several queens. Mating flights usually during late summer, sometimes into early autumn. Nationally: 13 species, including 1 species restricted to the Channel Islands. 7 species in Yorkshire.

L. flavus (Fabricius), *L. neglectus* Van Loon *et al.*, *L. niger* (Linnaeus), *L. platythorax* (Nylander).

L. fuliginosus (Latreille), 1928 (E); *L. mixtus* (Nylander), 1937 (E)
L. umbratus (Nylander), 1937. (E)

Genus **Formica** Linnaeus, 1758

Bicoloured red to dark brown or black ants (*F. lugubris*, *F. rufa*), or uniform brownish-black ants (*F. fusca*, *F. lemani*). Workers small to medium-size and queens and males medium-size (*F. fusca*, *F. lemani*) or workers small to medium-size and queens and males medium-size to large (*F. lugubris*, *F. rufa*). Nesting in banks, under stones or in tree stumps (*F. fusca*, *F. lemani*) or making mound nests of leaf and twig litter in clearings at the edges of pine and oak woodland (*F. rufa*), or semi-open woodland on undulating ground (*F. lugubris*). Colonies small with one or several queens and up to 500 workers (*F. fusca*, *F. lemani*), or large with many queens and 100,000 - 400,000 workers (*F. rufa*, *F. lugubris*). Forage 'milk' aphids besides being carnivorous and scavengers. Mating flights in late summer (*F. fusca*, *F. lemani*) or early summer (*F. rufa*). Colony foundation by a single queen or colony fission (*F. fusca*, *F. lemani*), or by colony fission and as temporary social parasites (*F. rufa* on *F. fusca*, *F. lugubris* on *F. lemani*). Nationally: 11 species with 4 species currently present in Yorkshire.

Formica fusca Linnaeus, *F. lemani* Bondroit, *F. lugubris* Zetterstedt, *F. rufa* Linnaeus.

Genus **Formicoxenus** Mayr, 1855

Reddish-yellow to brown ants. Queens small, workers and males very small to small. A guest ant in nests of *F. rufa* and *F. lugubris*. Small colonies with up to 100 individuals nesting in hollow twigs in the interior of the host colony. Does not prey on its host. Mating flight from late summer to early autumn. Nationally: 1 species, also present in Yorkshire.

F. nitidulus (Nylander).

Family **Pompilidae**

Solitary species known as spider or spider-hunting wasps. With their long legs they are usually seen making short rapid movements across bare ground and through short vegetation during warm, sunny weather. The female hunts for spiders as food for the larvae. See Day (1988) for details of prey. One spider is provided for each larva. The female paralyzes its prey and then usually carries or drags it across the ground to a place for temporary concealment or to a previously prepared nest site. Once the prey is in a cell an egg is laid on it and often the burrow to the cell is blocked. On hatching, the larva punctures the host's integument and begins to suck its blood. The spider eventually dies. Over-wintering is usually as a mature larva. There may be one or several generations a year. Nationally: 15 genera with 44 species (3 species restricted to the Channel Islands). 25 species in 11 genera in Yorkshire.

Genus **Dipogon** Fox, 1897

Medium-size black wasps. Aerial nesters in cavities, e.g. deserted insect borings in wood, hollow stems and mortar. Nationally: 3 species with 2 species currently present in Yorkshire.

D. subintermedius (Magretti), *D. variegatus* (Linnaeus).

Genus **Auplopus** Spinola, 1841

Medium-size black wasps with white marks on the face of the male. Make mud cells in sheltered situations such as under stones and in hollow plant stems. Several cells are built in contact with each other. Nationally: 1 species, also currently present in Yorkshire.

A. carbonarius (Scopoli).

Genus **Caliadurgus** Pate, 1946

Medium-size black wasps with some red on the anterior part of the gaster. Subterranean nester, excavating a short, vertical burrow in dry sandy, or sandy-clay, soils. Nationally: 1 species, also present in Yorkshire.

C. fasciatellus (Spinola). 1999.

Genus **Priocnemis** Schiødte, 1837

Small to large wasps. Black or black with red on the anterior part of the gaster. Subterranean nesters, often in clay soils, usually in woodlands. *P. parvula* nests in sandy soils including heathlands. *P. perturbator* and *P. susterai* also nest in lighter, including sandy, soils. Little is known about their nesting habits, but nests may contain several cells. Nationally: 13 species with 9 species in Yorkshire.

P. cordivalvata Haupt, *P. exaltata* (Fabricius), *P. gracilis* Haupt, *P. parvula* Dahlbom, *P. perturbator* (Harris), *P. schioedtei* Haupt, *P. susterai* Haupt.

P. fennica Haupt, 1994; *P. hyalinata* (Fabricius), 1991.

Genus **Pompilus** Fabricius, 1798

Small to medium-size black wasps with short grey hair. Subterranean nester in open sandy soils. The prey is temporarily buried whilst a nest burrow is partially excavated. The prey is then carried to the burrow. The burrow is extended and the prey placed in a terminal cell. Nationally: 1 species, also currently present in Yorkshire.

P. cinereus (Fabricius).

Genus **Agenioideus** Ashmead, 1902.

Small black wasps. Cavity nesters usually in an aerial position. Nationally: 2 species (1 species restricted to the Channel Islands). 1 species currently present in Yorkshire.

A. cinctellus (Spinola).

Genus **Arachnospila** Kincaid, 1900

Small to medium-size black wasps with red on the anterior part of the gaster. *A. anceps* and *A. trivialis* are subterranean nesters usually in sandy soils. The prey is hidden on a plant whilst a short burrow is excavated. *A. spissa* uses the nest burrow of its prey. Nationally: 7 species, with 3 species currently present in Yorkshire.

A. anceps (Wesmael), *A. spissa* (Schjødt), *A. trivialis* (Dahlbom).

Genus **Evagetes** Lepeletier, 1845

Medium-size black wasps with red on the anterior part of the gaster. Cleptoparasitic on other subterranean nesting Pompilidae. The female enters the cell of its host, eats the egg and substitutes its own. The cell is then closed. Nationally: 4 species (1 species restricted to the Channel Islands), with 1 species currently present in Yorkshire.

E. crassicornis.

Genus **Anoplius** Dufour, 1834

Medium-size to large wasps. Black or black with red markings on the gaster. *A. infuscatus* and *A. viaticus* are subterranean nesters excavating a short burrow in open, sandy soils. Prey is temporarily stored among vegetation whilst a burrow is excavated. *A. concinnus* and *A. nigerrimus* are crevice nesters. *A. concinnus* enlarges cavities beneath stones and *A. nigerrimus* uses hollow plant stems, snail shells and deserted aculeate burrows. Nationally: 5 species, with 4 species currently present in Yorkshire.

A. concinnus (Dahlbom), *A. infuscatus* (Vander Linden), *A. nigerrimus* (Scopoli), *A. viaticus* (Linnaeus).

Genus **Episyron** Schjødt, 1837

Medium-size to large wasps. Black with red on the hind leg and white markings on the gaster. Subterranean nester in open sandy soils. The prey is temporarily stored on a plant whilst the burrow is excavated. Nationally: 1 species, also currently present in Yorkshire.

Episyron rufipes (Linnaeus).

Genus **Ceropales** Latreille, 1802

Medium-size black wasps with yellow markings and reddish legs. Cleptoparasitic on other species of pompilid. The female intercepts the host pompilid carrying a paralysed spider. The host female is driven away, after which an egg is inserted into the lung-book of the spider. The host pompilid returns to her prey and continues to provision her nest. On hatching, the larva of *Ceropales* first destroys the host egg before feeding on the spider. Nationally: 2 species with 1 in Yorkshire.

C. maculata, 1950. (E)

Family **Vespidae**

Subfamily **Eumeninae**

Solitary, narrow-bodied wasps. Black with yellow or whitish-yellow bands and spots. They fold their fore-wings longitudinally when at rest. Adults are predatory, hunting the larvae of moths and beetles to feed their offspring. The female searches for a nest site, building a nest of a few cells and provisioning each cell with prey. One egg is laid at the end of a thread which is attached to the top of the cell before provisioning starts. After each cell is provisioned with several prey items it is sealed. Over-winters in the prepupal stage in the cell. One or more generations a year. Nationally: 9 genera with 23 species (including 1 species restricted to the Channel Islands and in addition 2 vagrant species). 12 species in 3 genera in Yorkshire.

Genus **Ancistrocerus** Wesmael, 1836

Medium-size to large wasps. Aerial nesters, as tube-dwellers in plant stems, e.g. bramble, elder; crevices, e.g. old walls, holes in dead wood, and man-made objects, e.g. hole of cotton reel, gap between books. Each nest consists of two to eight linearly-arranged cells separated from one another by clay partitions. *A. oviventris* builds its nest on the surfaces of walls or other hard materials. *A. scoticus* also builds cells entirely of clay in crevices, e.g. holes in the ground, behind bark, in hollow plant stems. Usually the nest consists of 3-5 cells made of clay. Nationally: 9 species, with 8 species in Yorkshire.

A. gazella (Panzer), *A. oviventris* (Wesmael), *A. parietinus* (Linnaeus), *A. parietum* (Linnaeus), *A. scoticus* (Curtis), *A. trifasciatus* (Müller).

A. antilope, (Panzer), 1973; (E) *A. nigricornis*, (Curtis), 1955. (E)

Genus **Odynerus** Latreille, 1802

Medium-size to large wasps. Subterranean nesters. Nationally: 4 species, with 1 species currently present in Yorkshire.

O. spinipes (Linnaeus).

Genus **Symmorphus** Wesmael, 1836

Medium-size to large wasps. Aerial tube-dwellers, usually in hollow plant stems, e.g. bramble, elder. Nationally: 4 species, with 3 species in Yorkshire.

S. bifasciatus (Linnaeus), *S. gracilis*.

S. crassicornis (Panzer), 1932. (E)

Subfamily **Vespinae**

The advanced eusocial wasps have an annual life-cycle in the British Isles. Adults feed on material containing carbohydrates such as tree sap, nectar, honeydew and steal honey from colonies of bumble bees. Overwintering fertilised queens emerge in the spring and build a nest from wood fibres which are macerated and mixed with saliva to form a pulp. The nest sites vary according to the species but may be underground, usually in an abandoned small mammal burrow, or aerial under an overhang, in a hollow tree, in a hedge, or inside a

building. The nest consists of combs of hexagonal cells which open downwards, and are surrounded by an envelope. The queen feeds the larvae on macerated insects and spiders. The first brood develop into adult workers. These workers build further combs and look after the brood hatching from more queen eggs. Later in the season combs of larger cells are built in which the new queens are reared. Males are usually reared in the smaller cells; but sometimes also in the large cells. Males and new queens leave the colonies and, after mating, the queens enter over-wintering sites in sheltered places e.g. under bark and stones, and the males die. The workers gradually all die. One species does not build its own nest but takes over, or usurps, a young colony, usually with just a few workers, of another species. Such a species is called a social parasite or a cuckoo. The cuckoo queen kills the host queen and uses the workers of the host species to rear a brood of new cuckoo queens and males. The cuckoo species does not produce workers. The queens of non-cuckoo species often attempt to usurp the queen of another colony, usually of the same species but sometimes of a different species. Nationally: 4 genera with 9 species, also in Yorkshire.

Genus **Dolichovespula** Rohwer, 1916

Large black and yellow wasps. Nests normally aerial on branches of trees or shrubs, in bird boxes, under eaves of a house or under overhanging earth banks. Colonies of *D. sylvestris* may be underground in existing cavities at, or near, the surface of the ground. Small colonies with, on average, about 200-300 workers at maximum size. Colonies usually from April to August. Nationally: 4 species, all currently present in Yorkshire. *Dolichovespula media* and *D. saxonica* are recent arrivals in Britain from Europe, and are still enlarging their ranges.

D. media (Retzius), *D. norwegica* (Fabricius), *D. saxonica* (Fabricius), *D. sylvestris* (Scopoli).

Genus **Paravespula** Blüthgen, 1938 (Now usually placed in genus *Vespula*).

Large black and yellow wasps. Nests usually in deep underground cavities which they enlarge. Sometimes nests are aerial in enclosed spaces, e.g. in cavity walls, attics, hollow trees. Large colonies with, on average, about 1600-2000 workers at maximum size. Colonies usually from April until October. Nationally: 2 species, also currently present in Yorkshire.

P. germanica Blüthgen, *P. vulgaris* (Linnaeus).

Genus **Vespa** Linnaeus, 1758

A large brown and yellow wasp usually known as a hornet. Aerial nests are found in hollow trees, roof spaces and outhouses. Some colonies are started in cavities underground but later re-located to aerial sites. Small colonies with, on average, about 190 workers at maximum size. Colonies usually from April until October. Nationally: 1 species, also currently present in Yorkshire.

V. crabro Linnaeus.

Genus **Vespula** Thomson, 1896

Large black and yellow wasps. *V. austriaca* is a social parasite on *V. rufa*. Nests usually in shallow underground cavities, often under the leaf litter or tufts of grass. A few nests are aerial e.g. in bird boxes, cavity walls, outhouses. Small colonies with, on average, about 160 workers at maximum size. Colonies usually from April until August. Nationally: 2 species, also in Yorkshire.

V. rufa (Linnaeus).

V. austriaca (Panzer), 1994.

Family **Sphecidae**

Genus **Ammophila** Kirby, 1798

Large black wasps with red markings on the gaster, which has an elongate petiole. Subterranean nesters in sandy soils. Short burrow ends in a single cell which is provisioned with the caterpillars of moths and sawflies. Nationally: 3 species, with 1 species restricted to the Channel Islands. 1 species currently present in Yorkshire.

A. sabulosa (Linnaeus).

Genus *Podalonia* Fernald, 1927.

Large black wasp with red markings on the gaster. Subterranean nesters in sandy soils. Burrow ends in a single cell which is provisioned with a single moth caterpillar. Nationally 3 species with 1 species restricted to the Channel Islands and 1 species in Yorkshire.

P. affinis (Kirby), 1974. (E)

Family **Crabronidae**

All species of this family are solitary wasps.

Genus **Dryudella** Spinola, 1843

Small black and red wasps. Subterranean nesters in sandy banks exposed to the sun. A slightly sloping burrow ends in a single cell which is provisioned with nymphs of Lygaeidae (heteropteran bugs). Nationally: 1 species, also currently present in Yorkshire.

D. pinguis (Dahlbom), 1993.

Genus **Tachysphex** Kohl, 1883

Medium-size wasps coloured black or black and red. Subterranean nesters in sandy soils exposed to the sun. The burrow of *T. pompiliformis* is short, leading to a few cells. The burrow of *T. nitidus* is long, ending in a single cell. Cells are provisioned with grasshopper nymphs. Nationally: 5 species (2 species restricted to the Channel Islands), 2 species currently present in Yorkshire.

T. nitidus (Spinola), *T. pompiliformis* (Panzer).

Genus **Trypoxylon** Latreille, 1796

Medium-size black wasps with the anterior tarsus and tibia in *T. clavicerum* largely reddish. Crevice nesters usually in aerial sites, e.g. hollow plant stems, beetle burrows in dry wood, but also in cavities in the soil. Cells separated by mud partitions. Cells provisioned with immature spiders. Parasites are *Pseudomalus* spp. and *Trichrysis cyanea*. Nationally 5 species, with three species currently present in Yorkshire.

T. attenuatum Smith, *T. clavicerum* Lapeletier & Serville, *T. figulus* (Linnaeus).

Genus **Crabro** Fabricius, 1775

Large black wasps with yellow bands on the gaster. Subterranean nesters usually in sandy soils fully exposed to the sun. The side branches of the burrow lead to several cells which are provisioned with flies. Nationally: 3 species, with 2 species currently present in Yorkshire.

C. cribrarius (Linnaeus), *C. peltarius* (Schreber).

Genus **Crossocerus** Lepeletier & Brullé, 1834

Small to medium-size wasps. Usually black, but a few species have yellow markings. Nationally: 22 species.

Subgenus **Crossocerus** s.str.

Usually subterranean nesters in sandy, sometimes clayey soils, but also in cavities in brickwork. Burrows lead to one (*C. ovalis*, *C. palmipes*), a few (*C. tarsatus*) or several (*C. pusillus*, *C. wesmaeli*) cells which are provisioned with small flies. 7 species currently present in Yorkshire.

C. distinguendus (Morawitz), *C. elongatulus* (Vander Linden), *C. ovalis* Lepeletier & Brullé, *C. palmipes* (Linnaeus), *C. pusillus* Lepeletier & Brullé, *C. tarsatus* (Shuckard), *C. wesmaeli* (Vander Linden).

Subgenus **Blepharipus** Lepeletier & Brullé, 1835

Aerial nesters in hollow stems and rotten dry wood. Burrows lead to one or several cells which are provisioned with small flies, except for *C. annulipes* which are provisioned with hemipterans, and *C. walkeri* with mayflies. 8 species currently present in Yorkshire.

C. annulipes Lepeletier & Brullé, *C. capitosus* (Shuckard), *C. cetratus* (Shuckard), *C. leucostomus* (Linnaeus), *C. megacephalus* (Rossius), *C. nigritus* (Lepeletier & Brullé), *C. walkeri* (Shuckard).

C. styrius (Kohl), 1997.

Subgenus **Ablepharipus** Perkins, 1913

Aerial nesters in decayed dry wood. Cells provisioned with small flies. 1 species currently present in Yorkshire.

B. podagricus (Vander Linden).

Subgenus **Hoplocrabro** Thomson, 1874.

Subterranean nester in sandy soils. Cells usually provisioned with flies. 1 species currently present in Yorkshire.

C. quadrimaculatus (Fabricius).

Subgenus **Cuphopterus** Morawitz, 1864

Aerial nesters in decaying dry wood. Cells provisioned with flies. 2 species currently present in Yorkshire.

C. binotatus Lepeletier & Brullé, *C. dimidiatus* (Fabricius).

Genus **Ectemnius** Dahlbom, 1845

Large black wasps with yellow markings. Aerial nesters in decaying dry wood. Burrow leads to several cells which are provisioned with flies. Nationally: 10 species, with 7 species currently present in Yorkshire.

E. cavifrons (Thomson), *E. cephalotes* (Olivier), *E. continuus* (Fabricius), *E. dives* (Lepeletier & Brullé), *E. ruficornis* (Zetterstedt), *E. sexcinctus* (Fabricius).

E. lapidarius (Panzer), 1995, *E. lituratus* (1852) (E)

Genus **Lindenius** Lepeletier & Brullé, 1834

Medium-size black wasps with a slight bronze sheen and yellow markings. Subterranean nesters, usually in sandy soils. Burrows with several branches each ending in a cell. Cells provisioned with heteropteran bugs or flies. Nationally: 3 species, with 2 species currently present in Yorkshire.

L. albilabris (Fabricius), *L. panzeri* (Van der Linden).

Genus **Entmognathus** Dahlbom, 1844

Small black wasps with restricted yellow markings. Subterranean nesters in sandy soils. Burrow with several branches each ending in a cell. Cells provisioned with larvae of chrysomelid beetles. Nationally: 1 species, also currently present in Yorkshire.

E. brevis (Vander Linden).

Genus **Rhopalum** Stephens, 1829

Small black wasps with reddish and yellow markings. Aerial nesters in hollow plant stems and beetle burrows in dry dead wood. Burrows lead to several cells which are provisioned mainly with small flies, but also homopteran bugs, psocids and psyllids. Nationally: 3 species, with 2 species currently present in Yorkshire.

R. clavipes (Linnaeus), *R. coarctatum* (Scopoli).

Genus **Oxybelus** Latreille, 1796

Small black wasps with ivory-white spots. Subterranean nesters usually in sandy soils. Cells provisioned with flies which are carried on the sting. Nationally: 3 species, with 1 species currently present in Yorkshire.

O. uniglumis (Linnaeus).

Genus **Mimumesa** Malloch, 1933

Medium-size black wasps. Aerial nesters in beetle holes in dry dead wood. Cells provisioned with homopteran bugs. Nationally: 5 species, with 1 species currently present in Yorkshire.

M. dahlbomi (Wesmael).

Genus **Mimesa** Shuckard, 1837

Medium-size black wasps with red markings on the gaster. Subterranean nesters in sandy soils. Burrow leads to several cells which are provisioned with homopteran bugs. Parasitized by *Elampus panzeri*. Nationally: 4 species, with 3 species currently present in Yorkshire.

M. equestris (Fabricius), *M. lutaria* (Fabricius).

M. bicolor (Jurine), 1979. (E)

Genus **Psenulus** (Dahlbom, 1843)

Medium-size black wasps. Aerial nesters in plant stems and dry, decaying wood. Cells provisioned with homopteran bugs. Nationally: 3 species, with 2 species currently present in Yorkshire.

P. concolor (Dahlbom), *P. pallipes* (Panzer).

Genus **Spilomena** Shuckard, 1838

Very small black wasps. Aerial nesters in plant stems and beetle holes in dry dead wood. Cells provisioned with thrips and possibly aphids. Nationally: 4 species, with 3 species currently present in Yorkshire.

S. differens, Blüthgen, 1953, *S. troglodytes* (Vander Linden).

S. beata Blüthgen, 1953.

Genus **Stigmus** Panzer, 1805

Small black wasps. Aerial nesters in plant stems and beetle holes in dry dead wood. Tunnel leads to several cells which are provisioned with aphids. Nationally: 2 species, also currently present in Yorkshire.

S. pendulus Morawitz, *S. solskyi* Morawitz.

Genus **Pemphredon** Latreille, 1796

Medium-size black wasps. Aerial nesters in plant stems and beetle holes in dry dead wood. Tunnel leads to several cells which are provisioned with aphids. *Trichrysis cyanea* could be a parasite of *P. inornata* and *P. lethifera*. Nationally: 6 species, with 4 species currently present in Yorkshire.

P. inornata Say, *P. lethifera* (Shuckard), *P. lugubris* (Fabricius), *P. morio* (Vander Linden).

P. austriaca (Kohl), 1903. (E)

Genus **Diodontus** Curtis, 1834

Small to medium-size black wasps. Subterranean nesters in sandy soils. Burrows with side branches lead to several cells which are provisioned with aphids. Nationally: 4 species also currently present in Yorkshire.

D. insidiosus Spooner, *D. luperus* Shuckard, *D. minutus* (Fabricius), *tristis* (Vander Linden).

Genus **Passaloecus** Shuckard, 1837

Small black wasps. Aerial nesters in plant stems and beetle holes in dry dead wood. Cells are separated by resin, or more rarely, mud partitions. Cells provisioned with aphids. *P. corniger* steals prey from other *Passaloecus* nests. Nationally: 8 species, with 6 species currently present in Yorkshire.

P. corniger Shuckard, *P. eremita* Kohl, *P. gracilis* (Curtis), *P. insignis* (Vander Linden), *P. monilicornis* Dahlbom, *P. singularis* Dahlbom.

Genus **Mellinus** Fabricius, 1790

Large black wasps with yellow or whitish-yellow markings. Subterranean nesters in sandy soils. Burrow leads to several cells which are provisioned with flies. Nationally 2: species (1 probably extinct). 1 species currently present in Yorkshire.

M. arvensis (Linnaeus).

M. crabroneus, (Thunberg) 1952. (E)

Genus **Nysson** Latreille, 1796

Medium-size black wasps with yellow markings. Cleptoparasites laying an egg on the host's prey. The larva, on hatching, first destroys the host's egg. Nationally: 4 species, with 3 species currently present in Yorkshire.

N. dimidiatus Jurine, *N. spinosus* (Forster), *N. trimaculatus* (Rossius).

Genus **Gorytes** Latreille, 1804

Medium-size black wasps with yellow markings. Subterranean nesters in a variety of soil types. Burrow leads to several cells which are provisioned with frog hopper nymphs. Nationally: 2 species, with 1 species currently present in Yorkshire.

G. laticinctus, (Lepeletier), *G. quadrifasciatus* (Fabricius).

Genus **Harpactus** Shuckard, 1837

Medium-size black wasps with white markings and partially red gaster. Subterranean nesters in sandy soils. Burrow leads to several cells which are provisioned with frog hoppers. Nationally: 1 species, also currently present in Yorkshire.

H. tumidus (Panzer).

Genus **Argogorytes** Ashmead, 1899

Large black wasps with yellow markings. Subterranean nesters in dry sunny situations. Burrow leads to several cells which are provisioned with frog hopper nymphs. Nationally: 2 species, also currently present in Yorkshire.

A. fargeii (Shuckard), *A. mystaceus* (Linnaeus).

Genus **Cerceris** Latreille, 1802

Large black wasps with yellow markings. Subterranean nesters usually in sandy soils. Burrow leads to several cells which are provisioned with beetles, usually weevils, and solitary bees. Nationally: 6 species, with 2 species currently present in Yorkshire.

C. arenaria (Linnaeus), *C. rybyensis* (Linnaeus).

Genus **Philanthus** Fabricius, 1790

Large wasps. Black with yellow markings. Subterranean nesters in sandy soils. Burrow leads to several cells which are provisioned with honey bee workers. Nationally: 1 species, also currently present in Yorkshire.

P. triangulum Fabricius.

The solitary and social bees

Like the solitary wasp species, females of solitary bees build and provision their nests which may be subterranean or aerial, or even in empty snail shells. Subterranean nesters may have specific requirements for their nest sites, e.g. banks or flat ground. Friable soil, often found in sandy soils but also dry clay or calcareous soils, is usually essential. The nest may consist of one or several cells. The cell walls are often of the surrounding material, e.g. soil or the *in situ* plant material, but may be lined with collected plant material, resin, mud or glandular secretions which harden to thin, cellophane-like, membranes. The larval food consists of nectar and pollen, sometimes with plant oils, and the cells are mass provisioned. The pollen is normally carried on specialised hairs on the propodeum, ventral gaster or hind legs, but sometimes in the crop of the female. Nectar is always carried in the crop. Some species collect pollen from a limited number of related plant species - these are called oligolectic bees. Others collect pollen from many plant species and are called polylectic species. When each cell is fully provisioned, an egg is laid and the cell sealed. There may be one or more generations each year. Several species are cleptoparasitic on other species of solitary bees. Some halictines are primitively eusocial. The queen rears a first brood, some of which, as adults, remain in the nest as workers and help the queen to rear a second brood of future queens and males.

Family Colletidae

Genus **Hylaeus** Fabricius, 1793

Solitary, small black hairless bees with short, blunt tongue, bilobed at the tip. Limited yellow or cream markings usually present on the head, thorax and legs. No hairs for carrying pollen, which is carried with nectar in the crop. Aerial nesters usually in dead stems, e.g. bramble, rose, dock, but also in crevices such as old beetle burrows and nail holes in wood, holes in walls and stones, and in crevices in the soil. *H. pectoralis* nests in old *Lipara* (Diptera) galls in *Phragmites* stems. Cells are arranged in a linear series and waterproofed by a cellophane-like material. Each cell with one egg which is laid on a semi-liquid food store of pollen and nectar. One generation a year, usually overwintering as a diapausing prepupa. Usually polylectic for pollen sources. Nationally: 12 species, with 6 species currently present in Yorkshire.

H. brevicornis Nylander, *H. communis* Fabricius, *H. confusus* Nylander, *H. hyalinatus*, Smith, *H. pectoralis* Förster, *H. signatus* (Panzer).

Genus **Colletes** Latreille, 1802

Solitary, medium to large, hairy, short-tongued bees. The tongue is broad and bilobed at the tip. Cuticle black, sometimes reddish posteriorly on first tergum. Conspicuous pale posterior bands of dense decumbent hairs present on the gaster. Pollen carried mainly in scopa on the tibiae, femora and sides of propodeum. Subterranean nesters in soil, soft mortar of walls and soft sandstone. Often nests are in large aggregations in sandy banks e.g. *C. succinctus* on the North York Moors. Burrow usually straight leading to several cells. Each cell has either a

short lateral burrow to the main burrow or main burrow terminating in a cluster of cells. Cells are lined and waterproofed with a cellophane-like material. The river bank at Beningbrough, Yorkshire with aggregations of *C. daviesanus*, becomes covered by flood water during the winter. Cells are provisioned with a semi-liquid store of pollen and nectar. The egg is attached to the upper wall of the cell. The cell is closed by a lid of cellophane-like material. One generation a year, generally passing the winter as a diapausing prepupa. Mainly oligolectic for pollen sources, e.g. *C. daviesanus* on Asteraceae, particularly *Tanacetum*; and *C. succinctus* mainly on *Erica* and *Calluna*. Bees of the genus *Epeolus* are cleptoparasitic on *Colletes*. Nationally: 9 species, with 5 species currently present in Yorkshire.

C. daviesanus Smith, *C. fodiens* (Geoffroy in Fourcroy), *C. halophilus* Verhoeff, *C. hederæ* Schmidt & Westrich, *C. succinctus* (Linnaeus).

Family **Andrenidae**

Genus *Andrena* Fabricius, 1775

Solitary, small to large subterranean nesting bees with short pointed tongues. Generally the cuticle is black except for some males with yellow markings on the head and some species with red markings on the gaster. The hair may be coloured white, grey, yellow or black. Sometimes with white or cream-coloured hair bands on the gaster. Pollen-carrying hairs present on the lateral surfaces of the propodeum, hind coxa, trochanter, femur and tibia. Nests may be isolated from each other or close together as an aggregation. Generally a nest consists of an entrance leading to a main burrow with shorter lateral burrows, each ending in a cell or cluster of cells. Females of *A. scotica* may nest communally, with several females sharing a common entrance. The cells are lined with a wax-like substance. The pollen balls are smooth and more or less spherical. One egg is laid on each pollen ball. Most species have a single generation a year, although a few have two generations a year when seasonal dimorphism may be shown. Spring species over-winter as adults, whereas summer species over-winter as diapausing prepupae. The two sexes emerge more-or-less at the same time, the males a few days earlier than the females. Most species are polylectic, but some are oligolectic for pollen sources. Nationally 68 species (1 species restricted to the Channel Islands), with 36 species currently present in Yorkshire.

A. angustior (Kirby), *A. barbilabris* (Kirby), *A. bicolor* Fabricius, *A. chrysoceles*, (Kirby), *A. cineraria* (Linnaeus), *A. clarkella* (Kirby), *A. denticulata* (Kirby), *A. fucata* Smith, *A. fulva* (Müller in Allioni), *A. fuscipes* (Kirby), *A. haemorrhoea* (Fabricius), *A. helvola* (Linnaeus), *A. humilis* Imhoff, *A. lapponica* Zetterstedt, *A. minutula* (Kirby), *A. nigriceps* (Kirby), *A. nigroaenea* (Kirby), *A. nitida* (Müller) *A. ovatula* (Kirby), *A. praecox* (Scopoli), *A. ruficrus* Nylander, *A. semilaevis*, *A. scotica* Perkins, Pérez), *A. subopaca* Nylander, *A. synadelpha* Perkins, *A. tarsata* Nylander, *A. thoracica* (Fabricius), *A. tibialis* (Kirby), *A. varians* (Kirby), *A. wilkella* (Kirby).

A. coitana (Kirby), 1991; *A. falsifica* Perkins, 1924 (E) *A. labialis* (Kirby) (E), 1971; *A. labiata* Fabricius, 1945; *A. pilipes* Fabricius (E), 1950; *A. similis* Smith, 1994.

Genus **Panurgus** Panzer, 1806

Solitary medium-size to large, subterranean nesting, short-tongued bees. Cuticle coloured black. Pollen-carrying hairs on hind tibia. Females nest in loose aggregations in bare or sparsely vegetated soils. Entrance of nest leads to a main burrow with lateral burrows, each ending in a terminal cell. The cells are lined with a wax-like material. The pollen balls are

smooth and more-or-less spherical. Overwinter as diapausing prepupae. Mainly oligolectic on yellow-flowered Asteraceae for pollen sources. Nationally: 2 species, with 1 species currently present in Yorkshire.

P. banksianus (Kirby). 1987. (E)

Subfamily **Halictidae**

Subterranean-nesting species with short, pointed tongues which may be solitary or eusocial. For solitary species the female establishes a nest in the spring with the males and new females emerging in the summer. After mating the males die and the females overwinter as diapausing adults. Eusocial species rear two broods a year. The first of these is reared by the queen, after which some workers remain in the nest to help the queen rear a second brood of males and new queens.

Genus **Halictus** Latreille, 1804

Small to large bees. Cuticle of some species, e.g. *H. rubicundus*, black, but metallic bronzy-green for other species, e.g. *H. tumulorum*. Gaster often with posterior white hair bands. Pollen-carrying hairs on the hind femur and tibia. Nest in aggregations. *H. rubicundus* and *H. tumulorum* may be solitary or eusocial. Nationally: 8 species (2 species restricted to the Channel Islands), with 2 species currently present in Yorkshire.

H. rubicundus (Christ), *H. tumulorum* (Linnaeus).

Genus **Lasioglossum** Curtis, 1833

Small to medium-sized bees.

Subgenus **Lasioglossum** s.str.

Probably all solitary species. Cuticle black. Polylectic for pollen sources. Nationally: 8 species, with 1 species currently present in Yorkshire.

L. lativentre, (Schenck) *L. leucozonium* (Schrank).

L. laevigatum (Kirby), 1966 (E); *L. quadrinotatum* (Kirby), 1935, (E)

Subgenus **Evyllaeus** Robertson, 1902

Cuticle black. Solitary (e.g. *L. fulvicorne*, *L. nitidiusculum*, *L. rufitarse*, *L. villosulum*) and eusocial (*L. albipes*, *L. calceatum*) species, although *L. calceatum* can also be a solitary species. All species probably polylectic for pollen sources. Nationally: 20 species (1 species restricted to the Channel Islands), with 9 species currently present in Yorkshire.

L. albipes (Fabricius), *L. calceatum* (Scopoli), *L. fratellum* (Pérez), *L. fulvicorne* (Kirby), *L. minutissimum*, (Kirby), *L. nitidiusculum* (Kirby), *L. punctatissimum* (Schenck), *L. rufitarse* (Zetterstedt), *L. villosulum* (Kirby).

L. parvulum (Schenck), 1907 (E); *L. pauxillum* (Schenck), 1987 (E).

Subgenus **Dialictus** Robertson, 1902

Cuticle bronzy-green or blue. Probably solitary, but some may be eusocial. Probably polylectic for pollen sources. Nationally: 4 species, also currently present in Yorkshire.

L. cupromicans (Pérez), *L. leucopus* (Kirby), *L. morio* (Fabricius), *L. smeathmanellum* (Kirby).

Genus **Sphecodes** Latreille, 1804

Small to medium-size cleptoparasitic bees usually on *Halictus* and *Lasioglossum*. *S. pellucidus* is a cleptoparasite of *Andrena barbilabris* and *S. rubicundus* on *A. labialis*. Sparsely hairy with black cuticle usually with red marks on the gaster. Females lack pollen-carrying hairs. The female enters the cell of its host and destroys the host's egg. Then she lays an egg on the pollen ball. Nationally: 17 species (1 species restricted to the Channel Islands), with 10 species currently present in Yorkshire.

S. crassus Thomson, *S. ephippius* (Linnaeus), *S. ferruginatus* von Hagens, *S. geoffrellus* (Kirby), *S. gibbus* (Linnaeus), *S. hyalinatus* von Hagens, *S. monilicornis* (Kirby), *S. pellucidus* Smith, *S. puncticeps* Thomson, *S. reticulatus* Thomson.

S. miniatus von Hagens, 1951. (E)

Subfamily **Melittidae**

Pointed short-tongued solitary bees. Nationally: 6 species in 3 genera.

Genus **Melitta** Kirby, 1802

Medium-size to large, subterranean-nesting, solitary bees. Black with white or tawny hair bands on the gaster. Claw-joint thickened. Pollen carrying hairs on the hind tibia and basitarsus. The main burrow leads to lateral burrows each ending in a cell. Pollen ball firm. Winter passed as a diapausing larva enclosed in a cocoon. Females oligolectic for pollen sources, e.g. *M. leporina* on clovers and vetches (Fabaceae). Nationally: 4 species, with 1 species currently present in Yorkshire.

M. leporina (Panzer).

Subfamily **Megachilidae**

Long-tongued solitary bees with a rectangular labrum. Pollen carrying hairs present on the ventral gaster except for the cleptoparasitic species. Nationally: 39 species (1 species restricted to the Channel Islands) in 9 genera.

Genus **Anthidium** Fabricius, 1804

A large solitary bee found in a wide variety of habitats including gardens. Black with gold spots on the gaster. Large males defend clumps of flowers used as food sources by the females. The large male attempts to mate with the foraging females. Small males move around the outside of the territories and attempt to steal matings from the large males. Aerial nests in dead wood, hollow stems and crevices in mortar. Cell walls and plugs to the cells formed from long silky plant hairs, hence the name of this bee as the 'wool-carder' bee. Nationally: 1 species also currently present in Yorkshire.

A. manicatum (Linnaeus).

Genus **Stelis** Panzer, 1806

Small to medium-size cleptoparasites on *Anthidium*, *Hoplitis* and *Heriades*. Black or brown, sometimes with paler hair bands or pale markings on the gaster. After finding the nest of the host, the female returns repeatedly to place an egg in each cell before the cell is closed. The larvae destroy the egg or young larva of the host. Nationally 4 species with 1 species currently present in Yorkshire.

S. punctulatissima (Kirby).

Genus **Chelostoma** Latreille, 1808

Small to medium-size black bees with elongated bodies. *C. florisomne* has white hair bands on the gaster. Aerial nesters in holes in dead wood and stems. Cells arranged linearly, separated by partitions of mud and sand grains stuck together by salivary secretions or nectar. Females oligolectic for pollen sources, e.g. *C. florisomne* on *Ranunculus*. Nationally: 2 species, with 1 species currently present in Yorkshire.

C. florisomne (Linnaeus).

Genus **Osmia** Panzer, 1808

Medium-size to large bees with unmarked black or metallic brown-green or blue cuticle. Aerial nesters in crevices. *O. caerulescens* and *O. leaiana* nest in wooden posts and mortar walls using chewed leaf pulp (leaf mastic) for the cell walls and partitions. *O. rufa*, besides nesting in wooden posts and mortar walls, also nests in snail shells and burrows in vertical soil banks, using mud for the cell walls and partitions. Females polylectic for pollen sources. Usually one generation a year. Overwinter as diapausing adults. Nationally: 11 species, with 3 species currently present in Yorkshire.

O. bicornis (Linnaeus), *O. caerulescens* (Linnaeus), *O. leaiana* (Kirby), *O. spinulosa* (Kirby).

Genus **Megachile** Latreille, 1802

Medium-size to large bees. Black, sometimes with white or cream hair bands on the gaster. Usually crevice nesters in aerial situations, e.g. decaying wood, woody stems, old masonry, but also in crevices under stones and in the soil. *M. circumcincta* is a subterranean nester in firm sandy soils. Females polylectic (e.g. *M. centuncularis*, *M. ligniseca*, *M. willughbiella*) or probably polylectic (e.g. *M. circumcincta*, *M. versicolor*) for pollen sources. The cells are made from cut pieces of leaves, or sometimes petals. Rectangular pieces are cut for the side walls and circular pieces for the end walls of the cell. Provisions are a semi-liquid mixture of pollen and nectar. One generation a year. Overwinter as diapausing prepupae within cocoons. Nationally: 8 species, with 6 species currently present in Yorkshire.

M. centuncularis (Linnaeus), *M. circumcincta* (Kirby), *M. leachella* Cutis, *M. ligniseca* (Kirby), *M. versicolor* Smith, *M. willughbiella* (Kirby).

Genus **Coelioxys** Latreille, 1809

Medium-size, relatively hairless bees with prominent white hair bands or spots on some of the gaster. The gaster is pointed in the female. Cleptoparasites on species of *Megachile* and *Anthophora*. A female cuts a slit in the host's cell, through which an egg is laid. The enormous curved jaws of the first instar larva are used to destroy the egg or young larva of the host. Later instars have normal size mandibles and feed on the host's provisions. Overwinter as prepupae in a cocoon. One generation a year. Nationally: 8 species (with 1 species restricted to the Channel Islands), with 4 species currently present in Yorkshire.

C. elongata Lepeletier, *C. inermis* (Kirby), *C. rufescens* Lepeletier & Serville.

C. quadridentata (Linnaeus), 19421. (E)

Family **Apidae**

Long-tongued solitary bees. Nationally: 71 species (including 4 species restricted to the Channel Islands) in 9 genera.

Genus **Nomada** Scopoli, 1763

Small to medium-size bees. Body sparsely hairy and cuticle marked with combinations of yellow, red and black bands or spots. Cleptoparasitic usually on species of *Andrena*. The female enters the open cell of the host and inserts its egg into the wall of the cell. The first instar larva kills the egg or young larva of the host with its large sickle-shaped mandibles. Afterwards the provisions are eaten. Pupae are not enclosed within a cocoon. May have one generation (e.g. *N. obtusifrons*, *N. roberjeotiana*, *N. rufipes*) or two generations (e.g. *N. fabriciana*, *N. flavoguttata*) a year. Sometimes the second generation has a very much reduced population (e.g. *N. goodeniana*, *N. marshamella*). Some species, usually with one generation a year, may persist into August (e.g. *N. lathburiana*, *N. panzeri*, *N. ruficornis*, *N. striata*); perhaps these later populations represent a partial second generation. Nationally: 32 species (including 4 species restricted to the Channel Islands), with 16 species currently present in Yorkshire.

N. fabriciana (Linnaeus), *N. flava* Panzer, *N. flavoguttata* (Kirby), *N. flavopicta* (Kirby), *N. fulvicornis* Fabricius, *N. goodeniana* (Kirby), *N. integra* Brullé, *N. lathburiana* (Kirby), *N. leucophthalma* (Kirby), *N. marshamella* (Kirby), *N. panzeri* Lepeletier, *N. robertjeotiana* Panzer, *N. ruficornis* (Linnaeus), *N. rufipes* Fabricius, *N. striata* Fabricius.

N. obtusifrons Nylander, 1991

Genus **Epeolus** Latreille, 1802

Medium-size bees cleptoparasitic on species of *Colletes*. Cuticle black with the thorax and gaster having conspicuous areas of white or cream-coloured patches of dense, very short hairs. The female enters an open cell and inserts an egg into the wall of the cell. The first instar larva, with its long curved mandibles, destroys the host's egg. The provisions are then eaten. No cocoon is spun. One generation a year. Nationally: 2 species, also currently present in Yorkshire.

E. cruciger (Panzer), *E. variegatus* (Linnaeus).

Genus **Anthophora** Latreille, 1803

Large bees. Black cuticle except the front of the male head which is yellow-marked. *A. plumipes* is usually a subterranean nester, but it also nests in old crumbling masonry. Nests usually of two or more burrows which end in short lengths of consecutively-arranged cells. Adults emerge from pupae in the late summer but remain in their cells until the following spring. *A. furcata* nests in dead wood. Nests usually consist of two or more parallel galleries. Cells formed from enlarging a part of a gallery. Overwinter as prepupae in cocoons. One generation a year. Nationally: 5 species, with 2 species currently present in Yorkshire.

A. furcata (Panzer), *A. plumipes* (Pallas).

Genus **Melecta** Latreille, 1802

Large cleptoparasitic bees on species of *Anthophora*. Black cuticle, often with distinct lateral patches of white hairs on some gaster segments. Female digs into the nest of its host and makes a small hole through the cell wall through which an egg is laid. The egg is laid on the inside of the wall of the cell. The hole in the cell is repaired with mud and the burrow entrance is re-plugged with soil. The first instar larva, with its long sickle-shaped mandibles, destroys the host's egg and other *Melecta* eggs or young larvae. The provisions are then eaten. Pupation occurs within cocoons. *M. albifrons* overwinter as adults within the cells of its host. One generation a year. Nationally: 2 species, 1 probably extinct, with 1 species currently present in Yorkshire.

M. albifrons (Forster).

The advanced eusocial bees of the family Apidae consist of the bumble bees and the honeybee. The bumble bees have an annual life-cycle very similar to that of social wasps. Queen bumble bees overwinter in subterranean burrows, in leaf litter or under bark. In the spring, according to the species, the queen initiates a nest either underground usually in an abandoned small mammal burrow, or at the surface of the ground under dry leaf litter. The queen makes a space in the nesting material of the small mammal or in the leaf litter and then builds a honey pot from wax secreted beneath her gastral sterna. She fills the honey pot with regurgitated nectar. Some eggs are then laid on a mass of pollen which is surrounded by a wax cell. The queen incubates the cell by lying across it. The larvae are progressively fed on a pollen-nectar mixture, the wax cell being gradually enlarged to accommodate the growing larvae. The first adults are workers which build further cells and forage for food. Some species, called 'pocket-makers', build wax pockets near the base of the wax cell into which the foragers deposit their loads of pollen to feed the larvae. This diet is supplemented by a pollen-nectar mixture regurgitated to the larvae through a small hole in the cell. In other species, called 'pollen-storers', the foraged pollen is stored in empty pupal cocoons or specially built wax cylinders. A pollen-nectar mixture is squirted into the larval cell through a hole in the wax covering. Further wax cells make an irregular-shaped nest. At pupation the larvae spin a silken cocoon. The wax from the cell is then removed and used to build further cells. Several species are social parasites; the cuckoo queen enters the colony of its host, kills the queen and uses the workers to rear new cuckoo queens and males. No cuckoo workers are reared. Queens of non-cuckoo bumble bee species, like the social wasps, also usurp colonies of the same, or different, species.

Genus **Bombus** Latreille, 1802

Large, hairy bumble bees which are eusocial except for subgenus *Psithyrus* which are social parasites on other bumble bees. Hair usually black with yellow, red, white or tawny bands. Pollen carried in the corbicula on the hind legs. Usually polylectic for pollen sources. *B. monticola* is associated with *Vaccinium* flowers on mountains and moorlands. *B. magnus* is associated with heather moorlands and *B. jonellus* with heaths and moors. Colonies vary from small (30-50 workers) to large (200 or more workers). Usually one generation a year with the fertilised queen overwintering. *B. pratorum*, *B. jonellus* and *B. hortorum* may have two generations a year. Parasitized by *Mutilla europaea*. Nationally: 25 species, with 17 species currently present in Yorkshire.

B. cryptarum (Fabricius), *B. hortorum* (Linnaeus), *B. hypnorum* (Linnaeus), *B. jonellus* (Kirby), *B. lapidarius* (Linnaeus), *B. lucorum* (Linnaeus) s.l., *B. magnus* Vogt, *B. monticola*

Smith, *B. muscorum* (Linnaeus), *B. pascuorum* (Scopoli), *B. pratorum* (Linnaeus), *B. terrestris* (Linnaeus).

B. barbutellus (Kirby), *B. bohemicus* (Seidl), *B. campestris* Panzer), *B. rupestris* (Fabricius), *B. sylvestris* (Lepeletier), *B. vestalis* (Geoffroy in Fourcroy).

B. distinguendus Morawitz, 1974 (E); *B. humilis* Illiger, 1968 (E); *B. ruderarius* (Müller), 1987 (E); *B. ruderatus* (Fabricius), 1954 (E); *B. soroeensis* (Fabricius), 1975 (E); *B. subterraneus* (Linnaeus), 1935 (E); *B. sylvarum* (Linnaeus), 1951. (E)

Genus *Apis* Linnaeus, 1758.

A. mellifera – Honeybee.

Further natural history information to about British aculeates is given in Gauld & Bolton (1996). Nixon (1954), Andrewes (1969) Michener (2000). O'Neill (2001) and Danforth *et al*, give more detailed information about the wasps and bees, particularly the solitary species. Keys to bee species are given in Else & Edwards (2018) and Falk (2015), to solitary wasps in Yeo & Corbet (1983), and Pomolidae in Day (1988) . Of the social species the ants are considered in Brian (1977) and Skinner & Allen (1996) with keys to species, the social wasps by Spradbery (1973) , Edwards (1980) with keys to species and Archer (2012) and the bumble bees by Alford (1975) and Prÿs-Jones & Corbett (1987), both with keys to species.

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